ON THE INHERITANCE OF COLOR IN THE AMERICAN HARNESS HORSE.

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In a study of the English thoroughbred horse C. C. Hurst[1] has shown that chestnut is recessive to bay and brown. He supposes that the presence of black in the coat is the dominant character. Now black, gray and most roan horses also have black in their coats, but 95 per cent. of the English thoroughbreds are bay, brown or chestnut, so that Hurst was unable to verify his supposition. The American trotting and pacing horse, however, a close relative of the English thoroughbred, exhibits colors in proportions much more favorable for an investigation of this kind. These proportions are about as follows: bay, 53 per cent.; black, 13 per cent.; brown, 15 per cent.; chestnut, 14 per cent.; gray, 3 per cent.; roan, 2 per cent.; dun, .1 per cent.

Perhaps before going further it will be well to give a brief discussion of these colors. According to Miss F. M. Durham, as quoted by W. Bateson,[2] there are three pigments, yellow, black and chocolate, concerned in the color of horses, as in mice, rabbits and other animals. Chestnuts have the yellow pigment alone.[3] Bays have both yellow and black pigments, and browns are only very dark bays, shading into the self-colored blacks on the other extreme. Grays have black hairs mixed with white ones, usually in a dapple pattern. Roans are of at least three types. The most common are the bay, red or strawberry roans, which have yellow-black hairs intimately mixed with white ones. The black, blue or gray roans appear to differ from grays chiefly in that their black and white hairs are more intimately mixed. The chestnut roans have yellow and white hairs. As will appear later the fact that there is no black in this class introduces a possible source of error into my calculations. However, these chestnut

[1] *Proc. Royal Soc.*, Vol. 77, B., 1906, p. 388.

[2] "Mendel's Principles of Heredity," p. 125.

[3] According to Bateson some chestnuts are really chocolates, but these are like the yellows in having no black.

roans are rare, forming something less than 10 per cent of the total number of roans seen on the streets of New York, and nearly all of those seen are heavy draught horses, so that I feel sure they are very rare indeed among blooded trotters. The official records do not distinguish between these three types of roans, but in the journals it is not rare to see a horse described as belonging to one of the two commoner classes, though I have never yet seen in them a reference to a chestnut roan. There are several types of duns, but, as appears in the list above, all are rare. In a few families duns seem to be dominant to bay, brown and black, and one was connected with gray, but beyond this I have found nothing about the color. Lastly there are a very few spotted trotters, but these are all poorly bred ones, with short pedigrees, and I have done nothing with them.

I have tried to show here that Hurst's discovery of the dominance of bay and brown to chestnut holds good for the American harness horse, and that gray, black and roan, or all other colors containing black, are also dominant to chestnut. In order to avoid confusion I shall call this dominant factor for the presence of black Hurst's factor. Apparently all trotters have the factor for chestnut, which I shall represent by *C*. This factor is hypostatic to all the others here mentioned. The factor next highest in the scale is that for black, or Hurst's factor, *H*, its absence being *h*. Next higher is that for bay, *B*, its absence being *b*. At the top stand the gray and roan factors, *G* and *R*. Now most horses have neither of these last two, and are therefore *ggrr*. A chestnut will always be *Chh*, but may have any combination of the other factors and their absences, since they produce no visible effect in the absence of Hurst's factor. Self blacks are *CHHbb* or *CHhbb*, since bay is epistatic to self black. Bays have one or two *C*'s, *H*'s and *B*'s. Grays have *C*, *H* and *G*, and roans have *C*, *H* and *R*. Whether these last two must have *B* or not is not clear. I shall discuss the three epistatic colors more fully and give my theory as to brown when I have presented the evidence as to Hurst's factor.

The chief authorities for the statistics and color pedigrees given here have been Wallace's "Year Book of Trotting and Pacing" and Wallace's "American Trotting Register," both of which are official records.

It is a recognized fact among the breeders of harness horses that certain stallions never produce chestnut foals. In *Wallace's Monthly* for February, 1880, there is an article by "Truth," in which he says: "I have learned that neither of the brothers [Volunteer and Sentinel] have ever sired a chestnut colt." W. H. Marrett, in the September, 1890, issue of the same paper, tells us that the two bay sires Volunteer and Electioneer never had chestnut foals. Both were by a bay sire (Rysdyk's Hambletonian, which appears in the first table below), one being from a bay mare, the other from a brown. In a sale catalogue issued in 1903 C. W. Williams says of the brown stallion Belsire: "His get are . . . bays, browns and blacks." This horse is a son of the Electioneer mentioned above and of a black mare whose sire was a black and dam bay. He is a full brother to the bay Chimes which appears in the table below, and to Bow Bells, bay, and St. Bel, black, both also probably homozygous.

I have found a good many sires homozygous for Hurst's factor. The small number of gray and roan sires in the table below is to be explained by the small number of those colors existing. It will be noticed that two of the number have one chestnut foal each recorded. Director's was found in an advertisement in a horse journal—obviously a poor authority, as the pedigree might easily have been false. That by Jay Bird is Cardenas, trotting record 2:26¼, from a chestnut mare. He is recorded as a chestnut by the "Year Book." But the "Year Book" does sometimes make mistakes in the matter of color. Among others I could mention is the case of the bay stallion Charley Wilkhurst, recorded as a gray gelding.[1] In this connection it is worth noting that Hurst found about 1 per cent. of exceptions recorded in his investigation, but was able to explain most of them by showing them to be probably mistakes.

[1]See *The Horse Review* for December 12, 1905, p. 1424.

TABLE OF SIRES HOMOZYGOUS FOR HURST'S FACTOR.

Stallion.	Color.	Sire's Color.	Dam's Color.	Foals.						
				Bays.	Blacks.	Browns.	Chestnuts.	Grays.	Roans.	All.
Chimes[1]	bay	bay	black	15	1	4	0	0	0	20
Electioneer[2]	bay	bay	brown	39	2	9	0	2	0	52
Happy Medium	bay	bay	bay	59	0	4	0	4	2	69
Rysdyk's Hambletonian	bay	bay	brown	40	0	8	0	2	0	50
Director	black	brown	bay	15	35	19	1	2	2	74
Gambetta Wilkes[3]	black	brown	brown	12	12	6	0	0	0	30
Oro Wilkes	black	black	black	15	3	4	0	0	0	22
Sable Wilkes	black	bay	black	23	19	7	0	0	0	49
Dictator	brown	bay	black	12	7	5	0	0	0	24
George Wilkes	brown	bay	brown or roan	12	5	3	0	0	1	21
Prodigal	brown	bay	bay	91	0	19	0	3	0	116
Conductor	gray	bay	gray	3	1	5	0	15	0	24
Pilot Medium	gray	bay	gray	19	0	5	0	61	1	116
Eagle Bird	roan	roan	brown	15	1	4	0	0	8	28
Jay Bird	roan	brown	roan	54	0	15	1	3	63	136
Margrave	roan	brown	roan	28	0	5	0	2	30	65

[1]Half of these foals from mares by the chestnut Mambrino King.

[2]Twenty-nine of these chestnut mares.

[3]Eleven of these from chestnut mares.

I have found only 69 cases of chestnuts being mated together, but in all these the result was chestnut. They are from the following stallions:

Chestnut Sire.	Color.		Number of Chestnut Foals from Chestnut Mares.
	Sire.	Dam.	
Nutwood	bay	gray	10
Robert McGregor	bay	bay	7
Attorney	bay	?	6
Daniel Lambert	bay	?	5
Elyria	chestnut	black	4
Hinder Wilkes	bay	chestnut	4
Mambrino King	black	?	4
Six different sires with two each			12
Eleven sires with one each			11
Total			69

The finding of foals from heterozygous sires and chestnut mares is a very slow and laborious task, but I have found some from the following stallions:

Stallion.	Color.	Foals from Chestnut Mares.	
		Chestnuts.	Total Found of all Colors.
Alcyone	bay	3	7
Axtell	bay	8	10
Boreal	bay	6	8
Guy Wilkes	bay	7	8
Norval	bay	1	6
Onward	bay	8	20
Red Wilkes	bay	8	14
Strathmore	bay	3	6
Total bay sires	bay	44	79
Grattan	black	1	4
Simmons	black	5	7
Total black sires	black	6	11
Alcantara	brown	2	8
Allerton	brown	8	17
Total brown sires	brown	10	25
Alcryon	gray	2	2
Re-election	gray	3	4
Total gray sires	gray	5	6
Grand Total		65	121
Expectation		60½	121

Here again I have been handicapped in working with gray and roan by the small number of sires of those colors, and also by the fact that most of the best known of those existing seem to be homozygous. However, I have found some sires of those colors which throw a fair percentage of chestnut foals, as shown in the following table, which shows all known foals. Two blacks are also included.

Stallion.	Color.	Chestnut Foals.	Foals of All Colors.
Bellini	black	3	17
Mambrino Patchen	black	3	16
Alcryon	gray	9	30
Pilot, Jr.	gray	4	20
Jay Hawker[1]	roan	1	20
Roan Wilkes	roan	3	10
Tom Hal, Jr.[2]	roan	1	15

[1] The one chestnut from Jay Hawker is scarcely to be doubted, as he is Country Jay 2:07¼, world's champion trotter under saddle, and one of the most prominent race horses of the season of 1909.

[2] This one chestnut also is not a doubtful one. His name is in fact Chestnut Hal.

It seems to me that we have here sufficient proof that Hurst's original supposition is right—that the dominant character is the black in the coat. However his idea that the black, if present, exists on the fetlocks, seems to me to be unjustified, as Joe Patchen, a heterozygous black, has white feet, though the white does not reach as far up as the fetlock on the left hind one. Grattan, another heterozygous black, also has three white fetlocks. It is not at all rare to see pictures of bays or browns with one foot or more white as far up as the fetlock or further. Here are some examples: bays—Capo, both hinds; Moko, right hind; Arlo Leyburn, left hind; Allerworthy, both lefts; Hail Cloud, right front; browns—Redlac, both hinds; The Harvester, left hind; Searchlight, both hinds. At least one of these (Moko) is homozygous.

In the case of the next factor, bay, a complication arises in regard to brown. As explained before the presence of bay is dominant to its absence and the color next below it in the scale is black. Brown is a color between these two, shading into both extremes. It seems that brown is usually a heterozygous color, represented by *CHBb*, but that bay also is quite often heterozygous, and that brown may occasionally be *either* of the homozygous types, *CHBB* or *CHbb*. This suggests the idea that the line between black and bay should be drawn somewhere near the black limit of brown. The obvious result of this complication is the creation of considerable confusion in the numerical proportions of the two colors. It is evident that, except for this complication and the appearance of some chestnuts, bay will act as though it were an ordinary dominant to black.

Below is a table showing twelve sires homozygous for the bay factor. Six of them are bays, and one is the only brown certainly known to be homozygous for this factor. Two are chestnuts, and therefore lack Hurst's factor. The other three are a gray and two roans, and it will be noted that all three of them appeared in the table of sires homozygous for Hurst's factor. They are not bays because they also bear other factors, as I shall explain later. Of the bays two are homozygous and four are heterozygous for Hurst's factor. The single black from Robert McGregor is Bobby Good, pacer, 2:11¼, out of a daughter of Ashland Wilkes.

Stallion.	Color.	Sire's Color.	Dam's Color.	Foals.						
				Bays.	Blacks.	Browns.	Chestnuts.	Grays.	Roans.	All.
Ashland Wilkes	bay	bay	?	90	0	0	19	5	0	114
Rysdyk's Hambletonian	bay	bay	brown	40	0	8	0	2	0	50
Happy Medium.	bay	bay	brown	59	0	4	0	4	2	69
Onward.....	bay	brown	bay	85	0	7	24	1	0	117
Red Wilkes.....	bay	brown	?	92	0	7	22	3	0	124
Sphinx.....	bay	bay	chestnut	30	0	5	9	4	0	48
Prodigal.....	brown	bay	bay	94	0	19	0	3	0	116
Axworthy.....	chestnut	bay	bay	33	0	2	32	1	4	72
Robert McGregor....	chestnut	bay	bay	42	1	1	30	2	1	77
Pilot Medium ..	gray	bay	gray	49	0	5	0	61	1	116
Jay Bird	roan	brown	roan	54	0	15	1	3	63	136
Margrave	roan	brown	roan	28	0	5	0	2	30	65

The mating together of blacks should produce only blacks and a few chestnuts, since chestnut is the only color hypostatic to black. However it does produce some browns and is recorded as producing occasional bays. The bays so far found are: Kipling 2:21¼, by Gambetta Wilkes ex Margaret W., and Gipsey Bel 2:30, by St. Bel ex Gipsey A. Now there is some reason to doubt the color of St. Bel. His dam was the black Beautiful Bells, but his sire was the bay Electioneer, and he is the only black among the eleven foals by Electioneer from black mares that I have found. Moreover, counting St. Bel, I have found only two black foals out of a total of 52 from Electioneer. Since Electioneer was homozygous for Hurst's factor this small proportion cannot be partly explained by supposing that more of the 52 would have been black had they had that factor. Neither is it possible to suppose that the small proportion is due to suppression by the gray or roan factor, since the 52 include only two grays and no roans. It looks very much as though Electioneer were homozygous for the bay factor. St. Bel died young, leaving few foals, so that I have been unable to get much data about his descendants. As to the other apparent exception, Kipling, I shall only call attention to the fact that neither he nor his dam are very well known. The following table shows foals from two black parents.

The case of foals from heterozygous sires and black mares is

Black Sire.	Foals from Black Mares.			
	Bays.	Blacks.	Browns.	Chestnuts.
Bellini	0	2	0	1
Gambetta Wilkes	1	3	0	0
Grattan	0	3	0	0
Patchen Wilkes	0	8	0	0
Sable Wilkes	0	7	1	0
Simmons	0	3	0	0
Nine others	1	8	3	0
Total	2	34	4	1

the one where the uncertainty about brown causes the most trouble. Since the presence of Hurst's factor is necessary before any of the three colors in question can appear I have left out the chestnut foals in the following table of foals from black mares.

Stallion	Color	Foals from Black Mares.		
		Bays.	Blacks.	Browns.
Axtell	bay	1	4	3
Guy Wilkes	bay	1	7	3
Alcantara	brown	1	3	0
Allerton	brown	0	3	3
Nutwood	chestnut	2	3	0
Total		5	29	9

The numbers in the above table are small, and, as in the similar case with Hurst's factor, I have supplemented it with one giving all known foals, chestnuts being again left out.

Stallion	Color	Foals				
		Bays.	Blacks.	Browns.	Grays.	Roans.
Bow Bells	bay	8	2	0	0	0
Directum Kelly	bay	7	2	2	0	0
McKinney	bay	14	4	8	0	2
Baron Wilkes	brown	44	10	28	0	1
Brown Hal	brown	34	10	15	2	4
Dictator	brown	12	7	5	0	0
George Wilkes	brown	12	5	3	0	1
Highwood	brown	24	5	8	0	0
American Star	chestnut	6	2	1	1	0
Mambrino King	chestnut	4	3	1	0	0
The Earl	chestnut	2	1	1	0	0
Conductor	gray	3	1	3	8	0
Pilot, Jr.	gray	3	2	1	10	0
Eagle Bird	roan	15	1	4	0	8

Now to turn to the gray factor. In the first place, I make no claims that all gray is epistatic to the four usual colors. Perhaps

it will be best to take up the grays by families, and I will first treat of those in which it is epistatic, and then of the one in which it seems not to be.

Most of the high-bred grays of to-day go back to Pilot, Jr., through an unbroken line of grays. This horse was a gray, son of a black sire and of a mare of untraced breeding whose color I have been unable to find. The gray sires in the next table all get their gray from him. This table includes all known foals except chestnuts, these being omitted for the same reason as in the last case. Since gray is an unpopular color it is safe to say that nearly all these foals were from recessive (*gg*) mares. I have so far found only one case of grays being mated together, and, since the produce of that mating was never heard from after racing, I know of no horse homozygous for the gray factor, *G*.

Gray Stallion.	Sire's Color.	Dam's Color.	Foals not Gray or Chestnut.	Gray Foals.
Bayard	gray	?	4	5
Pilot, Jr.	black	?	5	10
Pilot Medium	bay	gray	55	61
Re-election	bay	gray	12	15
Total			76	91

The following sires are all sons of gray members of the Pilot, Jr., family. Several of them have gray foals in this table, but all of these are from gray mares.

Stallion.	Color.	Foals				
		Bays.	Blacks.	Browns.	Grays.	Roans.
Lord Russell	bay	16	0	0	1	0
Peter the Great	bay	24	1	2	2	0
Darknight	black	5	2	2	0	0
Electricity	brown	10	1	7	1	0
Expedition	brown	46	3	10	5	0
Highwood	brown	24	5	8	0	0
Mambrino Russell	chestnut	6	0	3	0	0
Nutwood	chestnut	70	9	2	3	0

There can be little doubt that in the Pilot, Jr., family gray is an ordinary dominant, and there are other families where it seems to be, though there is not as much evidence. One of these goes back to the mare Sontag Mohawk, and through her probably to imported Messenger, the foundation of the breed of American

harness horses. Another goes to the mare Bashaw Belle, daughter of Young Bashaw, gray. Of the three horses below, Conductor is a son of Sontag Mohawk. Manager is a grandson of Bashaw Belle, and Alcryon is out of Lady Blanche, daughter of Privateer, both grays.

Gray Stallion.	Sire's Color.	Dam's Color.	Foals not Gray or Chestnut.	Gray Foals.
Alcryon	bay	gray	14	7
Conductor	bay	gray	7	8
Manager	chestnut	gray	11	12
Total			32	27

Eros and Walnut Hall, a brother and son, respectively, of Conductor, and both browns, have no gray foals among the 35 I have found.

There is one family in which gray appears not to be epistatic. The first member of the family that I know of is General Wilkes, gray, son of George Wilkes (an ordinary brown which appears in two of the tables already given and has nine different sons in them) and of a gray mare. This stallion had some gray foals, of whose descendants I have found no record. But he had two sons not gray which have produced many gray foals. They are Dispute, black, and Bobby Burns, bay. I am not sure of the color of the dams of any of Dipute's gray foals, but in the case of Bobby Burns some of them are from bay mares. Dispute's maternal color pedigree I do not know, but Bobby Burns is from Dixie, a bay daughter of the brown Dictator appearing in some of the first tables in this paper. The colors of all foals found from Dispute and Bobby Burns are:

Dispute: bay, 3; black, 2; gray, 4; all, 9.

Bobby Burns: bay, 40; black, 10; brown, 10; chestnut, 3; gray, 43; all, 106.

This is certainly a different kind of gray from the others just described, but I have not enough data to try to explain it.[1]

[1]In connection with the bay and gray factors I may quote the following from the pen of Professor Karl Pearson ("The Law of Ancestral Heredity," *Biometrika*, 1903, vol. 2, p. 214), though it was written about the English thoroughbred: "If black or gray coat-colour in horses were 'recessive,' when two blacks were mated we should expect only black offspring, but black can disappear for a generation or even two and then reappear. Or, take a case like that of a gray horse Viscount,

The last character I have to deal with is roan. This, like gray, is epistatic to the four usual colors in most families, but may not be in all.

Many of the roans of to-day go back to the old roan race-mare Lady Franklin, through her daughter Lady Frank and grandson Jay Bird, both roans. Jay Bird sired Eagle Bird, Jay Hawker, Allerton and Jackdaw, and Jay Hawker sired Jay McGregor. The following table shows all foals but chestnuts.

Stallion.	Color.	Foals.					
		Bays.	Blacks.	Browns	Grays.	Roans.	All not Roan.
Eagle Bird	roan	15	1	4	0	8	20
Jay Bird	roan	54	0	15	3	63	72
Jay Hawker	roan	6	0	0	0	13	6
Total		75	1	19	3	84	98
Jay McGregor	bay	11	1	5	0	0	17
Allerton	brown	32	8	20	2	1	62
Jackdaw	brown	9	3	12	1	0	25

Allerton's roan foal is from a roan daughter of Jay Bird.

Another family goes back to Laura Fair, roan, through her roan granddaughter Spanish Maiden. This last mare produced 1 bay and 3 roans, including the sire Margrave. Tom Hal, Jr., founded another family of roans, and another goes to the roan mare Tilla, which had 4 bay foals, 1 brown and 3 roans, the latter including Fred S. Wilkes. The Brown Hal appearing in the table below is a son of Tom Hal, Jr. Chestnut foals are omitted as before.

Stallion.	Color.	Foals.	
		Not Chestnut or Roan.	Roan.
Fred S. Wilkes	roan	13	8
Margrave	roan	35	30
Tom Hal, Jr.	roan	7	7
Total		55	45
Brown Hal	brown	61	4

where gray remained dominant for three generations only to disappear before the chestnut of the mare Blue Stocking in the Viscount and Blue Stocking filly Miss Johanna!" Just what that passage was intended to mean is a problem which I have not yet solved. What do blacks produce when mated together, and what has that to do with skipping a generation or so? And if a recessive cannot skip what can? Certainly not a dominant. What is to prevent us from supposing Viscount a heterozygote?

The roan and also the two gray foals of Brown Hal probably get their color from their dams, since in all cases these were daughters of roan or gray sires. As to the kind of roans these are I can only say that Margrave and one of his foals, and one of the foals of Tom Hal, Jr., are all red roans.

I have found six roan foals which had neither parent roan. One was from a dun mare. One was from two bays and another was from a chestnut and a bay, the chestnut being Robert McGregor, which almost certainly carried no gray factor. Another was from a bay sire and a chestnut dam. The other two each had a gray parent, and at least one of them was a black roan. Now only six roans produced by the thousands of cases of mating together horses not roan is a very small percentage. It is to be noticed that these six are not closely related. Even the two grays concerned are one Pilot, Jr., and one Sontag Mohawk. It seems to me probable that red roan at least is an ordinary dominant, and that all but one of the above cases are mistakes or exceptions. It is quite possible that all horses having the factor *R* are roan, the type of roan depending upon the color the horse would have been if he had not had that factor. This, if correct, explains away the difficulty presented in the next paragraph in so far as roan is concerned.

The relation between gray and roan is not clear. It seems probable that some of the *black* roans may be connected with gray, but an examination of the tables given above will convince one that, in general, the two colors are quite distinct. I have found only two instances of the mating together of grays and roans, and in both the result was gray. Of course much more evidence would be needed in order to find out how they act toward each other. The relation between these two factors and the bay factor is also not quite clear. It is evident that the presence of either can conceal bay, but whether or not either can appear in the absence of the bay factor is not certain. I am inclined to think that they can. If gray cannot we have an explanation of the gray foals from the black Dispute, but get no help in the much harder problem concerning his bay half-brother, Bobby Burns. One would expect to find some chestnuts carrying gray or roan factors (if the *ChhR* horses are chest-

nut roans there should be no chestnuts carrying the roan factor). With one possible exception in the case of each color I have found no such case. How unsatisfactory these two cases are will appear from the color pedigrees of the horses concerned.

Molly Morton, gray.	Banker Rothschild, brown.	Rothschild.
		Pilot Anna, gray.
	Lady Forrester, chestnut.	Royal George, chestnut.
		Belle of Saratoga, brown.
North Wind, roan.	Young Clay Pilot, bay.	Clay Pilot, bay.
		?
	Lola M., chestnut.	Roy Executor, brown.
		Light Dale, chestnut.

Summary.

This study of the pedigrees of blooded trotters indicates that the color of such horses is usually controlled by five factors, as follows. First, a factor for chestnut, *C*, present in all the horses studied. Second, a factor for black, Hurst's factor, *H*, epistatic to the factor *C*, and hypostatic to the three following. Third, a factor for bay, *B*. Fourth, a factor for roan, *R*. Fifth, a factor for gray, *G*. *R* or *G* inhibits *B* if it is present, but whether they depend upon its presence for their own appearance or not is not clear.

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